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## The role of dispersal constraints in the assembly of salt-marsh communities

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# *Chapter 1*

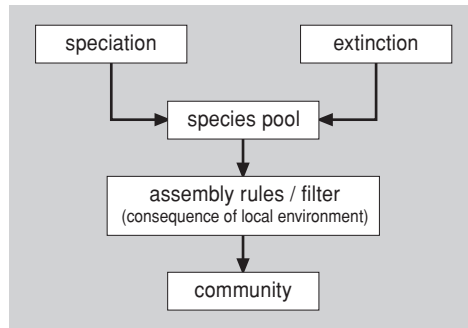
## **Introduction**

## Dynamics of Community Assembly

The study of constraints on community development has a long history dating back to the early twentieth century, when ecologists such as Clements (1916; 1936) and Gleason (1917; 1926) were already debating ‘organismic’ vs. ‘individualistic’ models of community development (Booth & Larson 1999). The dichotomies in their debate (deterministic vs. stochastic processes, local vs. regional scales) are still echoed in the current discussion on this subject in community ecology. After decades of investigating community structure in relation to local physical conditions and consequent influences on species interactions, ecologists are returning to the idea that local communities must be considered within the larger geographical and historical scales in which they are embedded in order to be fully understood (Ricklefs 1987). In this thesis, community structure is defined as patterns of species composition and species abundance in communities.

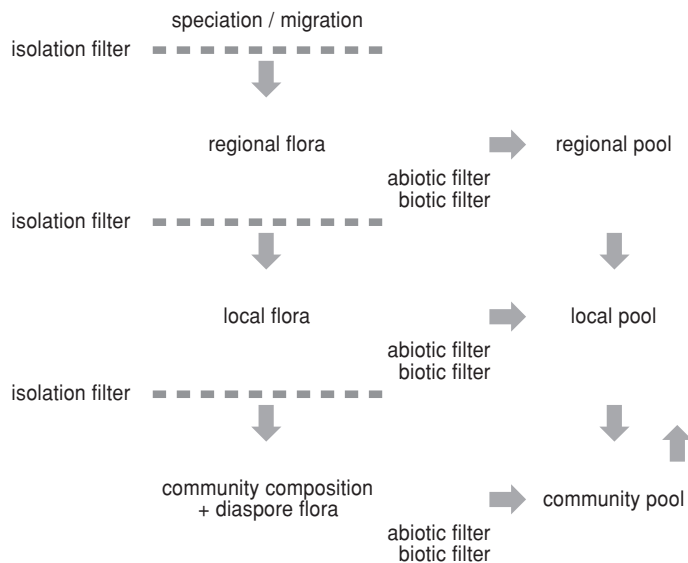
Dispersal filters may influence community assembly *per se* or through interactions with internal dynamics (*i.e.* species interactions) (Belyea & Lancaster 1999). The dispersal of some species may be dependent on close physical association with other species, so that the arrival of co-dispersers may not be independent (Chambers & MacMahon 1994; Belyea & Lancaster 1999). Species may be able to overcome constraints of dispersal over space by producing a bank of dormant propagules, which may remain viable for long periods of time (Thompson *et al.* 1997). Chance events during dispersal and the unique historical circumstances of sequence of arrival at a site may strongly affect species composition of communities through priority effects (Morin 1984; Barkai & McQuaid 1988; Drake *et al.* 1993; Grover 1994; Law & Morton 1996; Blaustein & Margalit 1996; Wilbur 1997; Belyea & Lancaster 1999). Even given identical conditions, communities with different histories may not converge (Drake 1990). In this Introduction, I will briefly discuss some current conceptual models of community assembly and show how I will use adaptations of these models as a framework to explore dispersal filters on the assembly of coastal salt-marsh communities.

In a simple conceptual model proposed by Keddy (2000), communities are generated from a pool of potential colonists (*i.e.* species pool) through a filtering process (Fig. 1.1). The filters, or hierarchy of filters, select for or against certain traits and ‘assembly rules’ specify which set of traits will be filtered out in a specified habitat. Biotic filters may include species interactions such as competition and predation/herbivory (Diamond 1975; Belyea & Lancaster 1999), whereas abiotic filters are characterized by the physical environment (Keddy 2000). The formation of the species pool, a large-scale process which is determined by rates of speciation and extinction, is considered to lie outside community ecology in the realm of evolutionary ecology in this model and the emphasis lies on the role of local filters in determining community structure.



**Figure 1.1** Conceptual model of community assembly, where the local environment filters out species from the species pool, thereby creating a community (after Wiens 1983; Keddy 2000).

In contrast, the species-pool concept (Pärtel *et al.* 1996; Zobel 1997; Zobel *et al.* 1998) explicitly addresses scale and scale-dependent dispersal of species. Pools of potential colonists are hierarchically arranged by the spatial scale over which they operate: regional, local and community (Fig. 1.2). The regional scale theoretically encompasses the geographical distribution of the community of interest (*i.e.* target



**Figure 1.2** Diagram of species-pool concept showing the role of processes at different scales in determining community composition (after Zobel 1997).

community). The local scale covers a single landscape type and species from the local species pool are assumed to disperse relatively quickly into the target community. The species associated with a community are referred to as the community species pool and it includes the species present in a community as well as the diaspore bank and rain. Species pools at all scales are pre-sorted in that they only include species which are capable of coexistence within the target community. However, the actual determination of species pools is still in its infancy and can be difficult to apply (Zobel *et al.* 1998; Srivastava 1999; Wolters *et al.* 2005b).

Of course, all species in a species pool do not normally arrive simultaneously at a given site but usually arrive sequentially, one or a few species at a time (Morton & Law 1997). Community assembly can be viewed from a historical perspective, incorporating turnover of species as invaders arrive and residents disappear over time. By considering the production of an existing community state through intermediate states, community organization can be explored as it emerges (Drake 1990). Thus, the concept of community assembly is integrated with the older but clearly related concept of succession.

## **Dispersal filters in the assembly of plant communities**

One seemingly straight-forward way to detect the effects of dispersal constraints on the species composition of plant communities is to disperse seeds artificially into sites and then to examine the consequences as is done in seed sowing experiments. Seed-sowing experiments can manipulate effects of seed limitation on species abundance or species distribution (seed augmentation and seed introduction, respectively, in Turnbull *et al.* 2000). In a review of seed sowing experiments, around 50 % of 27 seed-augmentation studies indicated constraints of seed limitation on species abundance (Turnbull *et al.* 2000). Seed limitation tended to occur more often in early-successional communities and species typical of the early-successional stages (Turnbull *et al.* 2000). However, seed limitation can result from multiple causes, such as poor distribution of seed sources (adult plants), low density of seed sources and low seed production (all of which are filters at the community scale), in addition to poor dispersal (Levine & Murrell 2003). Seed-augmentation experiments alone cannot distinguish between these potential causes. Results are easier to interpret for seed-introduction studies, where the seed sources are absent from communities. In 13 studies of seed introductions incorporating data from approximately 100 species, 53% of them indicated seed limitation on the distribution of species (Turnbull *et al.* 2000). Thus, about half of the seed-addition experiments reviewed in Turnbull *et al.* (2000) indicated possible dispersal constraints on both species abundance and composition in plant communities.

## Filters in the assembly of salt-marsh communities

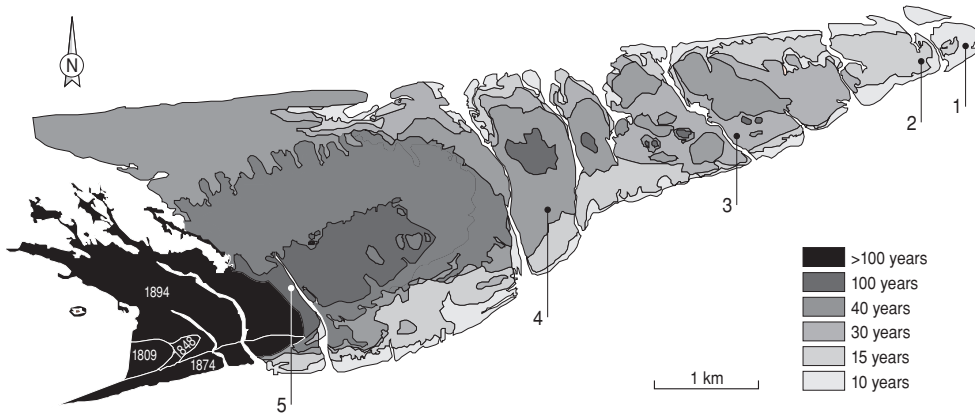
Salt-marsh communities have been used to demonstrate both biotic and abiotic filters in community assembly. Wilson and Whittaker (1995) suggested that the assembly rule of guild proportionality was demonstrated in a Welsh salt marsh. Members of the same guild or functional group are assumed to compete more with each other than with species in another guild (Pianka 1980). Consequently, the proportion of species from different guilds tends to remain constant (Wilson & Roxburgh 1994; Morris & Knight 1996). Competition between species in the canopy for light, and the different functional roles of broad and narrow leaves in canopy structure, was an important biotic filter in salt-marsh communities.

Keddy (2000) suggested another important filter, salinity, on the species composition of salt-marsh communities. When considering salinity as an abiotic filter, species can be screened and then ranked in relation to a single trait: salinity tolerance. If the salinity level of a local site is known, it is possible to predict which species from the species pool could potentially become established. However, both the studies described above concentrated solely on local processes and did not explore the potential role of dispersal filters in structuring salt-marsh communities.

Despite evidence that tidal action can disperse seeds considerable distances (action radius of tens of kilometers in Koutstaal *et al.* 1987), the few empirical studies conducted on seed dispersal in salt marshes indicate that the species composition of plant communities are potentially constrained by dispersal (Rand 2000; Wolters *et al.* 2005a). Further support of this conclusion comes from results of salt-marsh restoration sites, where former reclaimed lands were re-exposed to tidal inundation when sea walls were breached. When salt-marsh species were present locally, restoration sites generally acquired more of these species than when potential donor communities were located far away (Wolters *et al.* 2005b).

## Salt-marsh chronosequence as model system

Salt marshes on the Dutch island of Schiermonnikoog provide a unique opportunity to study the dynamics of community assembly due to a well-developed chronosequence reconstructed from aerial photographs and old maps (Olff *et al.* 1997). Sea currents and resulting erosion/sedimentation patterns have caused the island to move eastwards over time so that salt-marsh communities of progressive ages are found adjacent to each other (Fig. 1.3). The topography of these coastal barrier marshes is determined primarily by relief patterns in the sandy subsoil, which were formed by wind processes and subsequently fossilized, rather than sedimentary processes influenced by tidal water (de Leeuw *et al.* 1993). The eleva-



**Figure 1.3** Map of chronosequence of salt-marsh communities on Schiermonnikoog. Numbers represent location of communities of different ages: 10 years, 15 years, 30 years, 40 years and 100 year.

tion of the sandy subsoil ranges from 25 cm to 125 cm above mean high tide, whereas the sedimentary layer that lies above the sandy subsoil is only 2 cm to 16 cm in depth (Olff *et al.* 1997). Successional dynamics in species composition differ between elevational ranges (Olff *et al.* 1997) so that a proper chronosequence is observed by comparing sites at the same base elevation (sandy layer).

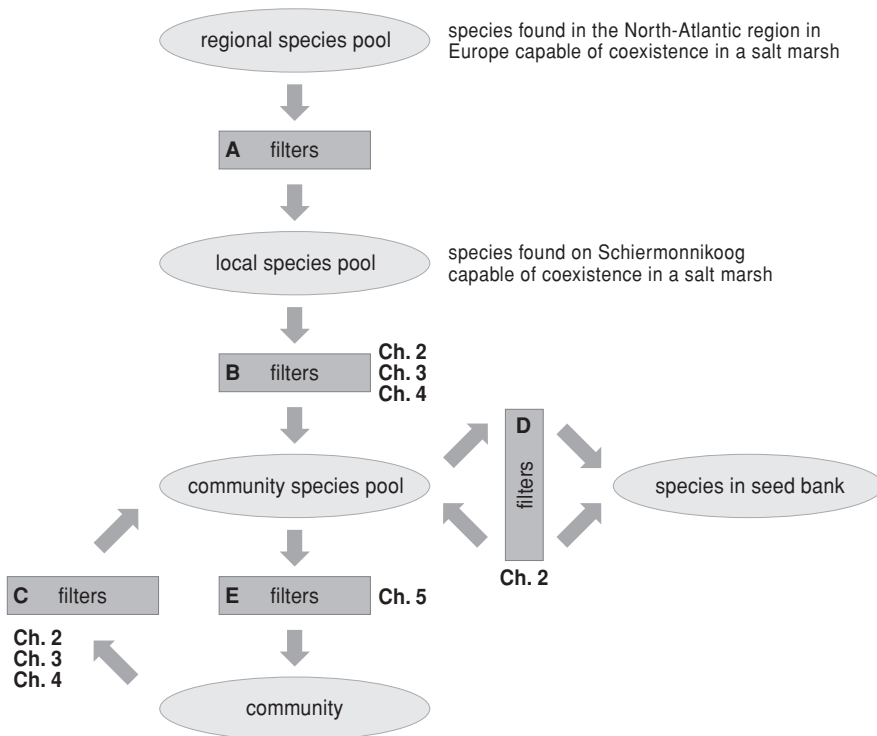
Studies of the species composition of salt-marsh communities at this site have concentrated on possible effects of biotic filters (*e.g.* competition, herbivory), abiotic filters (*e.g.* nutrient availability) and interactions between these two groups (*e.g.* herbivory and nitrogen mineralization, fertilization by faeces) (van de Koppel *et al.* 1996; Olff *et al.* 1997; van Wijnen & Bakker 1997; van Wijnen & Bakker 1999; van Wijnen *et al.* 1999; Kuijper *et al.* 2005; Kuijper & Bakker 2005; van der Graaf 2006). In short, most of these studies have concentrated on the effects of local filters on community development. However, results of a study on soil seed banks and seed composition of driftlines suggested that dispersal filters occur over both space and time (Wolters & Bakker 2002).

## Outline of thesis

Using the chronosequence of salt-marsh communities on Schiermonnikoog, I will examine the role of different dispersal filters in the dynamics of community assembly in this thesis. For many plant species, dispersal often occurs at the stage of the seed, although dispersal through vegetative propagules is also possible.

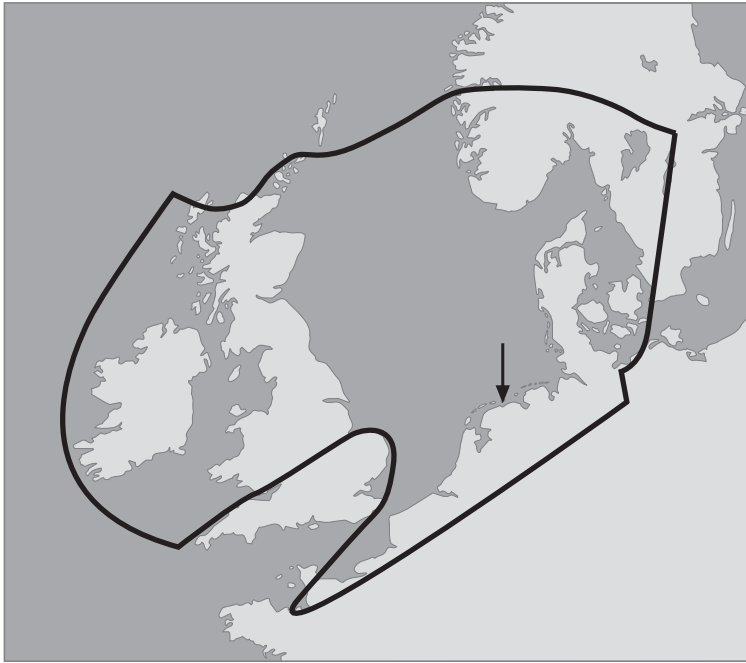
Dispersal filters over space can operate at both the regional (A in Fig. 1.4) and local scales (B in Fig. 1.4). The production of seeds can reinforce and maintain the membership of a species once it joins a community (C in Fig. 1.4). Dispersal filters over time are influenced by the burial, survival and exhumation processes of seed reserves in the soil (D in Fig. 1.4). Once a seed reaches a community, local filters governing a myriad of processes, such as seed retention, germination, competition, facilitation, herbivory, attack by pathogens, abiotic stress and disturbance, will determine whether that species will establish in the community or not (E in Fig. 1.4).

The regional scale is defined as that covering the central North-Atlantic region in Europe, that spans from Scotland and southern Scandinavia to northern France following Dijkema *et al.* (1984) and Wolters *et al.* (2005b) (Fig. 1.5). The salt-marsh communities on the south-eastern coast of Schiermonnikoog (*Oosterkwelder*), which are not grazed by livestock, delineate the local scale. Multiple communities along the chronosequence will be used to study the community scale.



**Figure 1.4** Conceptual framework for exploring constraints in the assembly of salt-marsh communities.





**Figure 1.5** Biogeographical area for which the regional species pool is defined (after Dijkema *et al.* 1984; Wolters *et al.* 2005b). Arrow refers to the position of Schiermonnikoog.

In Chapter two, I explain how the relationship between the species composition and species abundance of the community (established vegetation) and soil seed bank can be used to predict constraints on community assembly. A descriptive approach, using surveys of the vegetation, soil seed banks and seed production along the chronosequence, is combined with results from a burial experiment in order to examine the relative strength of filters on community assembly involved in dispersal (B in Fig. 1.4), seed burial and survival (D in Fig. 1.4) and seed production (C in Fig. 1.4).

In Chapter three, the potential roles of biotic (hares, geese) and abiotic (tidal water) filters in constraining dispersal are compared. I will use a descriptive approach, comparing the seeds found in the droppings of hares and geese to those caught on seed traps along the chronosequence, to study the effectiveness of these dispersal vectors. In addition, I will use an experimental approach with feeding trials of captive animals to study the effect of ingestion by these small herbivores on seed survival and germinability. Seeds found in droppings and on seed traps may reflect seed sources available in the community as well as those that result from local dispersal (B & C in Fig. 1.4).

I explore further the factors constraining movement of seeds by tidal water in Chapter four by comparing the effect of normal tides (deterministic) and storm surges (stochastic) on seed-rain patterns along the chronosequence. Mainly descriptive methods are used, supplemented by an experiment on the differential effects of water movement originating from the sea coast and creeks on seed movement. As in Chapter three, dispersal filters (B in Fig. 1.4) as well as community-level filters on seed availability (C in Fig. 1.4) are examined.

In Chapter five, I study the factors that influence seed retention, the opposite but complementary process to that examined in Chapter four. Experiments were conducted both in a field and laboratory setting to explore the process by which morphological traits of seeds are filtered by abiotic (tidal water) and biotic factors (vegetation structure of a community) (E in Fig. 1.4). Vegetation structure, as opposed to community structure, refers to physical properties such as height, biomass, shoot density and stiffness.

Finally, the synthesis in Chapter six will use data presented in Chapters two to five to evaluate the role of dispersal filters in constraining the composition and abundance of salt-marsh communities.

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